J Arid Land (2023) 15(1): 63–76
https://doi.org/10.1007/s40333-023-0001-z

Science Press Springer-Verlag

Biocrust-induced partitioning of soil water between grass and shrub in a desert steppe of Northwest China

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Abstract: Maintaining the stability of exotic sand-binding shrub has become a large challenge in arid and semi-arid grassland ecosystems in northern China. We investigated two kinds of shrublands with different BSCs (biological soil crusts) cover in desert steppe in Northwest China to characterize the water sources of shrub (*Caragana intermedia* Kuang et H. C. Fu) and grass (*Artemisia scoparia* Waldst. et Kit.) by stable ^{18}O isotopic. Our results showed that both shrublands were subject to persistent soil water deficiency from 2012 to 2017, the minimum soil depth with CV (coefficient of variation) <15% and SWC (soil water content) <6% was 1.4 m in shrubland with open areas lacking obvious BSC cover, and 0.8 m in shrubland covered by mature BSCs. For *C. intermedia*, a considerable proportion of water sources pointed to the surface soil. Water from BSCs contributed to averages 22.9% and 17.6% of the total for *C. intermedia* and *A. scoparia*, respectively. *C. intermedia* might use more water from BSCs in rainy season than dry season, in contrast to *A. scoparia*. The relationship between shrub (or grass) and soil water by $\delta^{18}O$ shown significant differences in months, which partly verified the potential trends and relations covered by the high variability of the water source at seasonal scale. More fine roots at 0–5 cm soil layer could be found in the surface soil layer covered by BSCs (8000 cm/m^3) than without BSCs (3200 cm/m^3), which ensured the possibility of using the surface soil water by *C. intermedia*. The result implies that even under serious soil water deficiency, *C. intermedia* can use the surface soil water, leading to the coexistence between *C. intermedia* and *A. scoparia*. Different with the result from BSCs in desert areas, the natural withdrawal of artificial *C. intermedia* from desert steppe will be a long-term process, and the highly competitive relationship between shrubs and grasses also determines that its habitat will be maintained in serious drought state for a long time.

Keywords: desert steppe; biological soil crusts; water resource; *Caragana intermedia*; *Artemisia scoparia*

Citation: YANG Xinguo, WANG Entian, QU Wenjie, WANG Lei. 2023. Biocrust-induced partitioning of soil water between grass and shrub in a desert steppe of Northwest China. Journal of Arid Land, 15(1): 63–76. https://doi.org/10.1007/s40333-023-0001-z

1 Introduction

In northern China, arid and semi-arid grassland ecosystems are threatened by desertification, and use of desert shrubs as sand-binding vegetation to restore such areas has been carried out in around 6×10^6 hm^2 over the past 60 a. However, sand-binding vegetation can reduce the soil water content of deep soil layers, leading to its dieback and mortality due to water stress (Li et al., 2014). Thus,

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Received 2022-10-13; revised 2022-11-24; accepted 2022-12-09

maintaining the stability of exotic sand-binding shrub has become a large challenge (Li et al., 2013).

The senescence of exotic sand-binding species and the reappearance of native species might not be avoidable (Li et al., 2014). However, the process may vary in different regions. For example, the inflection point of shrub-grass replacement, wherein the senescence of exotic shrubs is followed by the reappearance of native grasses, has been recorded at around 30–40 a after shrub plantings where the annual precipitation is about 200 mm (Li, 2005), or 10–20 a where annual precipitation is around 400 mm (Zuo et al., 2009). However, in desert steppes with the precipitation of around 300 mm where shrub (*C. intermedia*) has been replanted to restore sandy grassland, the shrub has remained the dominant species for more than 40 a without a significant increase in plant diversity (Yang et al., 2015). As a result, a binary vegetation structure dominated by the shrub and grass (*A. scoparia*) is common in the region (Zhao et al., 2015; Chen et al., 2019).

Soil water deficiency would drive the competition between shrubs and grasses for shallow soil water (Ehleringer et al., 1991), with upper and lower layer coexistence strategy (Le Roux et al., 1995) weakened. As a result, shrub degradation is not always avoidable. However, differences in root configuration among different shrub species and across life stages lead to variable use of water sources among individual shrubs in adapting to arid and semi-arid grassland ecosystems (Jia et al., 2012; Huang and Zhang, 2015; Zheng et al., 2015). For example, shrubs growing in the Mu Us Sandy Land of China can successfully compete to delay the emergence of grasses as the dominant species during later successional stages (Liu et al., 2010). In addition, the succession process is also related to disturbances, environmental factors such as precipitation, soil type, and other variables, indicating specificity of eco-hydrologic processes in different regions (Li et al., 2017). The different succession processes mentioned before reflect possible differences in the intensity and mode of shrub-grass competition for shallow soil water among different regions. However, to our knowledge, there are still few studies on the water source and competitive relationship between exotic *C. intermedia* and native grasses, especially in combination with stable isotope studies.

In arid regions, biological soil crusts (BSCs) are important factors affecting hydrological process and vegetation succession. Studies have shown that compared with bare soil, soil water infiltration decreases when the soil was covered by BSCs, and more water from precipitation being constrained in the shallow soil layers (i.e., shallowing soil hydrological processes) (Li et al., 2010; Zhang et al., 2015). In the Tengger Desert of China, the appearance of BSCs accelerates the decline of re-vegetated shrubs and the recovery of local shallow-rooted grasses (Li, 2005). However, in the Negev Desert of Southern Israel, moss crusts scarcely influence precipitation infiltration, and do not lead to shrub death (Kidron, 2014a). During severe droughts, BSCs even can provoke the death of certain annual plant species (Kidron, 2014b). Due to the differences in soil properties and crust types, the influence of BSCs on vegetation-hydrological processes are highly variable in different regions (Li et al., 2010; et al., 2012), and debate remains regarding the vegetation-hydrological effect of BSCs. The effects of BSCs on the exotic shrub *C. intermedia* and native species in the desert steppe of China have yet to be specifically analyzed.

C. intermedia is an important species for restoring sandy grassland, now which also faces the challenge of stability maintenance in the desert steppe. The different processes of shrub-grass replacement reflect potential specificity of ecological-hydrological mechanisms in this region. In order to investigate these mechanisms, we selected two examples of exotic *C. intermedia* shrublands with notable differences in BSCs coverings, and examined soil hydrological processes and water sources for the shrub and dominant grass *A. scoparia*. We aimed to describe the effect of BSCs on water sources of *C. intermedia* and *A. scoparia*, and deeply understand the stability of the exotic shrub in the region.

2 Materials and methods

2.1 Study area

The study area was located in a semi-arid desert steppe of Yanchi County, Ningxia Hui Autonomous Region of China (37°47′–37°57′N, 107°22′–107°33′E; Fig. 1). The annual mean

temperature is 8.1°C and mean annual precipitation ranges from 250 to 350 mm, with more than 62% of total precipitation occurring between July and September. Annual sunlight is 3124 h and potential evaporation is 2897 mm. The frost-free period lasts about 165 d. The main soil types of the region are sierozem, loess, and aeolian sandy soil. In general, the growth season for plants is from April to October, the precipitation and soil water condition often changed significantly before and after July. The period before July is called dry season with little precipitation and shallow soil water deficiency, except for more water in deep soil just from the supplies of precipitation in last year. The period after July is therefore called rainy season with more precipitation and good soil water condition in shallow layers.

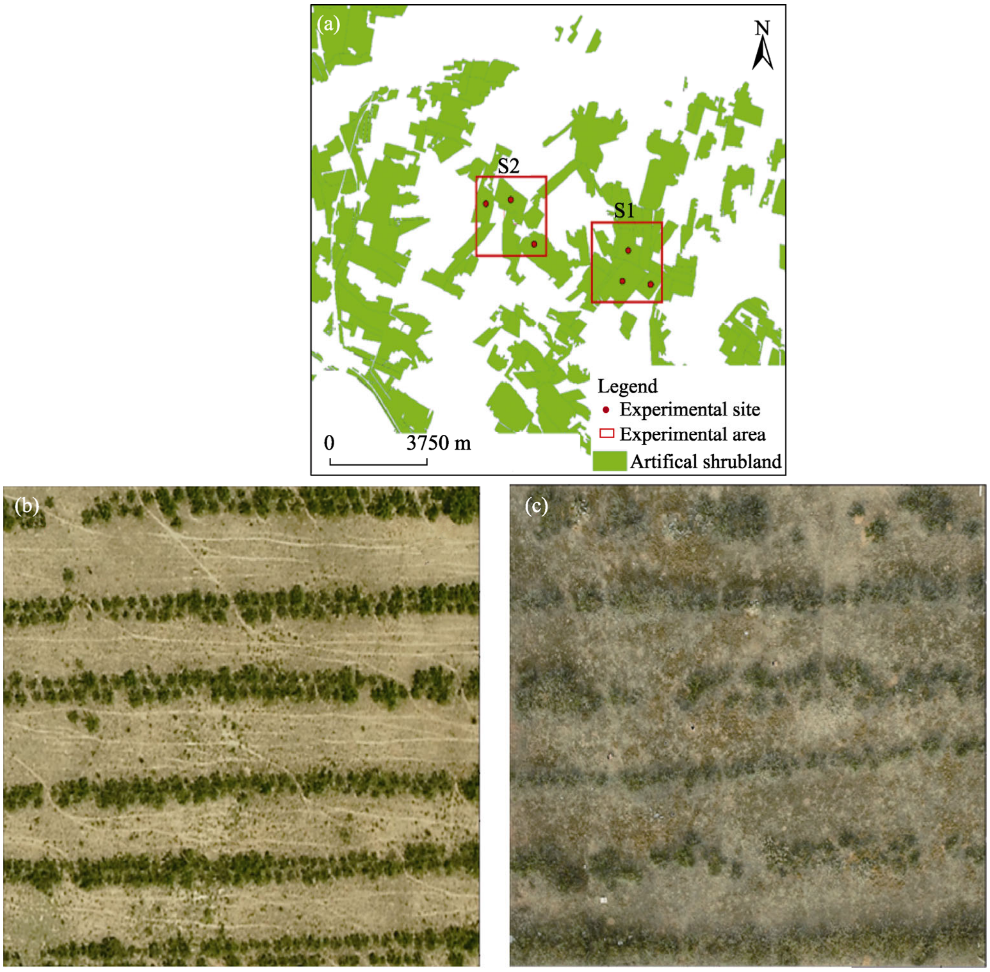

Fig. 1 Location of the experimental site (a), landscape and habitat characteristics of the shrubland (b and c). (b), S-CK, shrubland without BSCs (biological soil crusts) cover; (c), S-BSC, shrubland with BSCs cover.

The region is a typical transition zone between the Mu Us Sandy Land and the Loess Plateau. While there is considerable heterogeneity of climate, soil, and plants in the region, there has also been serious environmental destruction caused by human activity such as overgrazing of livestock. *C. intermedia* was extensively planted to restore these areas beginning in the 1970s, and the areas presently are more than 2×10^5 hm^2. Most of *C. intermedia* planted before the 1990s have reached maturity, and soil water deficiency and individual senescence has followed (Song et al., 2014; Yang et al., 2015).

C. intermedia is typically planted in a belt with two lines, spaced 1 m apart and 6–8 m between belts, and oriented perpendicular to the primary wind direction in winter and spring (Zuo et al.,

2006). The native vegetation of the area varies greatly due to differences in the degree of desertification and grazing disturbance. In general, most native species are annual plants adapted to sandy environments, such as *A. scoparia*. Most perennial grasses are only found in small soil patches scattered within the sandy grassland matrix.

2.2 Sampling design

Two *C. intermedia* shrublands with different BSCs covering were considered (Fig. 1). One shrubland lacked obvious BSCs cover (S-CK), while open areas of another shrubland were covered with BSCs (S-BSC). Shrub coverage was 23.5% in S-CK and 21.8% in S-BSC, without obvious differences (Table S1). Reduction of shrubs individuals was more obvious in S-BSC, with light damage to the canopy. *A. scoparia* was the dominant grass species in both shrublands, forming a single binary community with *C. intermedia*. Both shrublands had sandy calcareous soil in surface with similar qualities (Table S2). BSCs in S-BSC were composed primarily of moss, with traces of lichen, and covered 57% of the ground with an average thickness of 2 cm. Their color differed between the arid and rainy seasons, becoming gray in the dry season and green in the rainy season. Within each shrubland, we selected three 100 m×100 m sampling plots, and randomly chose five *C. intermedia* individuals and five subplots within different belts (one every other belt), 1.5 m from the edge of the belt. As shown in Figure 1, the belt just means the planting lines of shrub.

Both shrublands were planted in the 1980s over about 10 a. The oldest shrubland was around 40 a. Although these areas were subject to a mean grazing intensity of 1 sheep/hm^2, this varied widely over space and time. According to our investigation in the study area, when herders are reliant on livestock as their main income, higher grazing intensity is common, and BSCs in the shrubland are rare, such as in S-CK. However, some herders may give up grazing temporarily due to economic or other factors, or may sublease meadow to achieve rotation grazing. Therefore, these shrublands may be temporarily idle, giving BSCs a chance to develop, such as in S-BSC.

2.3 Soil moisture monitoring

In the sampled plots, 6 transparent plastic pipes for time-domain reflectometry (TDR) probes (HD2-TRIME/T3, IMKO Device Ltd., Ettlingen, Germany) were vertically installed in the soil, 1.5 m from the edge of the belt, to measure soil moisture from 0–300 cm layer in 20 cm intervals. Measurements were made every 15 d during the growing seasons from 2012 to 2017. Natural grassland without *C. intermedia* was also sampled to serve as control (CK). At the same sites, surface soil moisture was monitored from August 2015 at layers of 3 and 8 cm. These measurements were used to obtain average soil moisture at 0–5 and 5–10 cm, respectively. These sensors have a resolution of 0.001 m^3/m^3, estimated accuracy 0.02 (±0.03) m^3/m^3, ranging from 0 to 1 m^3/m^3. Installation of probes followed a protocol outlined in Chamizo et al. (2013), and was completed in August 2015. At each site, a U30 Soil Moisture Logger system was installed, and data was collected every 30 min using a HOBO Micro Station system (Onset Co., Bourne, Massachusetts, USA). Standard calibration equations were used to obtain measures of volumetric water content (Cobos and Chambers, 2010). Daily soil moisture was considered the average of the 30-min soil moisture records in a day.

2.4 Water sources for *C. intermedia* and *A. scoparia*

To further determine the role of BSCs in the water sources, and according to the main sources of soil water for plants based on the pre-test results and the limitation of the linear mixed model (the sources should be less than five; Dawson, 1993), we adjusted the sampling method of soil water during 2016–2017 based on four sources: (1) BSCs at 0–2 cm layer, (2) shallow soil from 2–30 cm layer, (3) middle soil from 30–70 cm layer, and (4) deep soil more than 70 cm layer, until reaching the impermeable parent material horizon. During 2016–2017, 9 sampling events in different months were completed. The sampling dates in dry season were May, June, and early July, then in rainy season were end July, August, and September. For each sampling event, three replicate samples of plants or soil were collected, yielding 27 samples in all.

During each sampling event, nine xylem samples were collected from two-year-old *C. intermedia* twigs without green parts. Nine xylem samples of root and stem joints from different *A. scoparia* individuals were also randomly selected. All bark and phloem were removed, and samples were pooled and transferred to glass vials sealed with parafilm, and stored in a portable cooler. At the same time, different layers of soil were sampled using a hand auger with 35 mm diameter, sealed, and stored. All samples were subsequently kept in a –20°C freezer prior to water extraction.

Water extraction and isotopic ^{18}O analyses were performed at the China Academy of Forestry. Eighteen samples for *C. intermedia* (seven in the dry season and eleven in the rainy season), and twelve samples for *A. scoparia* (five in the dry season and seven in the rainy season) were used to analyze water sources, meeting the requirements of the linear mixed model. IsoSource software package (Phillips and Gregg, 2003) was used to quantify the contributions of multiple water sources of different soil layers for *C. intermedia* or *A. scoparia*.

2.5 Fine root distribution in 0–10 cm soil layer for *C. intermedia*

The fine roots distribution of *C. intermedia* in S-BSC at layers of 0–5 and 5–10 cm was investigated in 2016. To examine the relative effects of BSCs, we established two kinds of root sampling plots away from the shrub belts used in the above experiments. One used three replicate 4 m×4 m plots with BSCs reserved, and the other used three replicate plots with BSCs removed completely in April 2016. To avoid the influence of grasses, we removed all grasses within each plot in August 2016. The plots were regularly maintained by manually removing new seedlings prior to root sampling. In October 2016, three 0.2 m×0.2 m subplots in each plot were established, and whole soil samples from 0–5 and 5–10 cm layers were collected. Fresh fine roots of *C. intermedia* with 0.5–2.0 mm diameter were extracted, and the root length was measured in field. Parts of fine roots less than 0.5 mm in diameter were discounted due to the associated difficulty in recognizing and collecting them (Fig. S1).

2.6 Statistical analyses

Statistical analyses were performed using SPSS v.20.0 statistical software (SPSS Inc., Chicago, USA). T tests were used to determine statistically significant differences (α=0.05) in root length between plots, and the differences of $\delta^{18}O$ among soil and plants. A time-depth contour map of soil moisture in different years was created using the Surfer v.13.0 software (Golden Software Inc., Colorado, USA), and used to analyze dynamics and trends in soil moisture during 2012–2017.

CV (coefficient of variation) values of soil moisture in the upper layers were greater than in deeper layers in general, for the disturbance of seasonal precipitation. We defined the soil moisture of some soil layer as relatively stable when the average value of CV_i (the coefficient of variation in soil moisture at the i^{th} soil layer) during 2012–2017 was lower than 15%. According to the variation of soil moisture in 0–300 cm layer during 2012–2017, the depth of the uppermost soil layer, whose average CV_i during 2012–2017 was lower than 15%, and SWC (soil water content) was lower than 6%, was considered empirically the maximum depth affected by precipitation, or the starting depth for soil water deficiency in the study area. When this depth was lower, soil water deficiency was regarded as more serious.

The daily difference in soil moisture in surface soil (0–5 cm layer) relative to the lower layer (5–10 cm layer) was calculated as follows:

$$ISSM = (SWC_5 - SWC_{10}) / SWC_{10} \times 100, \quad (1)$$

where ISSM is the daily increment of surface soil moisture (%); SWC_5 is the percent volumetric soil water content at 0–5 cm layer, and SWC_{10} is the percent volumetric soil water content at 5–10 cm layer. When the surface soil has a higher water holding capacity, precipitation infiltration will be delayed, leading to a higher water content relative to the lower layer for a certain duration. Under continuous monitoring of soil moisture, ISSM could be considered a simple indicator to measure dynamic changes in hydrological states in the surface soil, e.g., shallowing soil

hydrological processes.

3 Results

3.1 Soil moisture dynamics in 0–300 cm layer from 2012 to 2017

There were significant spatial and temporal differences among S-CK, S-BSC, and CK (grassland) (Fig. 2). From 2012 to 2017, soil water contents both in S-CK and S-BSC showed continuous decreasing trends, while natural grassland did not show similar changes. Soil water content in 0–60 cm layer in S-BSC was higher than that in S-CK, but the relation was opposed when the layer was more than 60 cm. Mean values during 2012–2017 indicated that the minimum soil layer with CV<15% and SWC<6% was 1.4 m for S-CK, and 0.8 m for S-BSC (Fig. S2). During most of the observation period, soil water deficiency was most evident in S-BSC, where the moisture of the soil layers below 1.0 m was always reliably within <6%.

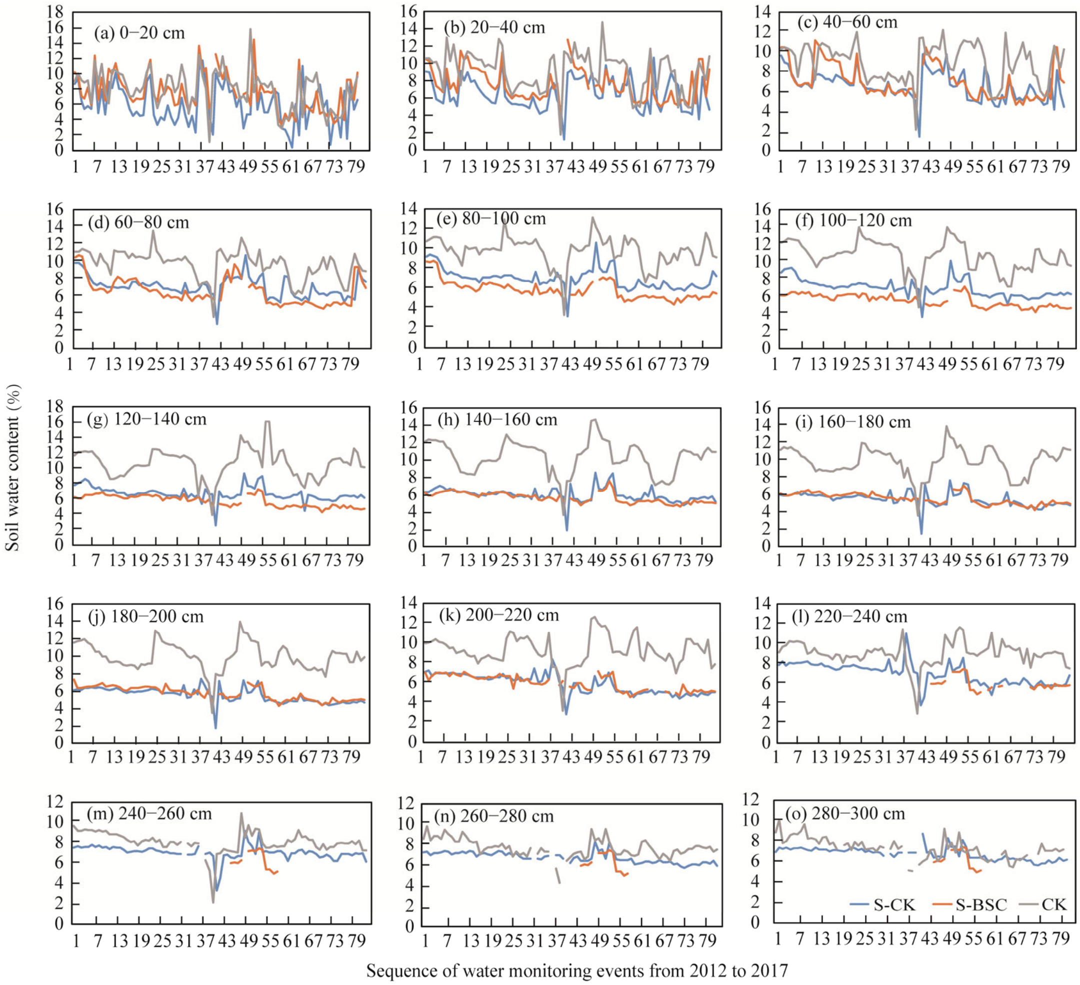

Fig. 2 Soil water contents in 0–300 cm (a–o) layer from 2012 to 2017. S-CK, shrubland with BSCs (biological soil crusts) cover; S-BSC, shrubland with BSCs cover; CK, natural grassland without replanted *Caragana intermedia*.

3.2 Daily surface soil moisture dynamics

The relative water content of the surface soil layer (0–5 cm) was consistently higher than the lower layer (5–10 cm) in S-BSC, but was lower or nearly equal to the lower layer in S-CK (Fig. 3). The relative increment in the ISSM was higher under the covering of BSCs (S-BSC: 14.67%

in mean, varying from –59.26% to 355.19%), indicating that BSCs retained more precipitation and led to greater relative residence time of water at the surface. Where there was no BSC cover, ISSM was greatly reduced (S-CK: –5.08% in mean, varying from –32.74% to 37.49%). This was a typical case of shallowing soil hydrological process under the covering of BSCs.

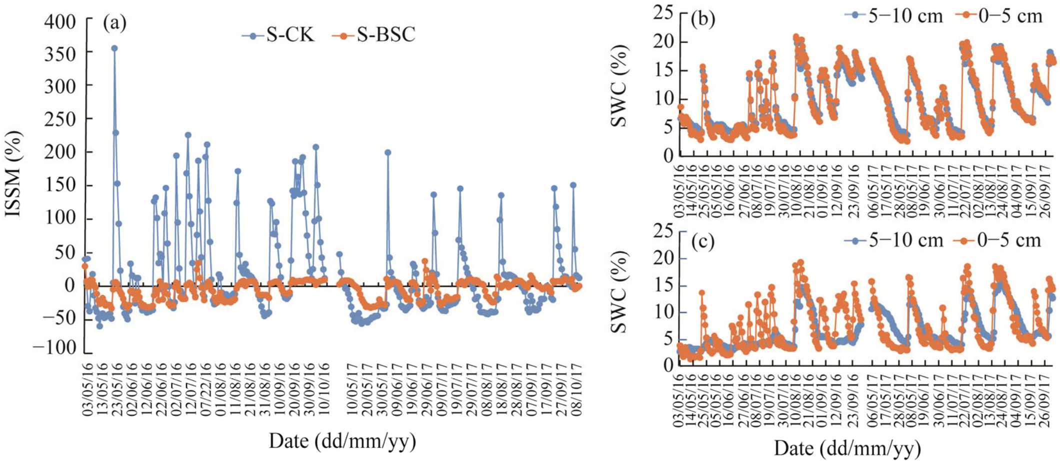

Fig. 3 Daily time series of relative increment in surface soil moisture (ISSM) in S-CK and S-BSC (biological soil crust) plots in the growth seasons (from May to October) during 2016–2017. (a), ISSM in S-CK and S-BSC; (b), SWC (soil water content) in 0–5 and 5–10 cm soil layers in S-CK; (c) SWC in 0–5 and 5–10 cm soil layers in S-BSC. S-CK, shrubland without BSCs cover; S-BSC, shrubland with BSCs cover.

3.3 Water uptake for *C. intermedia* and *A. scoparia*

To further understand the role of BSCs in water resource used by *C. intermedia* and *A. scoparia*, we collected water samples of BSCs (0–2 cm layer) and restricted soil water sampling to the shallow (2–30 cm layer), middle (30–70 cm layer), and deep (>70 cm) layers from 2016 to 2017 (Table 1). On average, BSCs were a source of 22.9% of water for *C. intermedia* and 17.9% for *A. scoparia*. The water from 0–30 cm contributed nearly 60% of the resources for both *A. scoparia* and *C. intermedia.*

Table 1 Average proportional water uptake from four potential soil sources for *Caragana intermedia* and *Artemisia scoparia*

Species	Index	Water source			
		Surface (0–2 cm)	Shallow (2–30 cm)	Middle (30–70 cm)	Deep (>70 cm)
Caragana intermedia (n=18)	Average (%)	22.9	34.3	22.8	20.0
	CV (%)	62.5	58.6	63.4	41.5
	Range (%)	0.0–55.6	9.5–80.4	2.7–63.3	2.2–33.1
Artemisia scoparia (n=12)	Average (%)	17.9	41.6	22.1	18.0
	CV (%)	81.3	73.9	108.2	67.1
	Range (%)	3.7–47.2	8.3–90.7	1.2–76.1	3.0–36.0

Note: CV, coefficient of variation.

More variation in *C. intermedia* water resource use was observed in the dry season than in the rainy season (Fig. 4). On average, more water was taken up from BSCs by *C. intermedia* in the rainy season, but not by *A. scoparia*. The greater uptake by *A. scoparia* from BSCs occurred in the dry season. The differences of water sources of *A. scoparia* between rainy season and dry season was related with its root growth dynamics (Fig. S3). However, the water resources in dry season between *C. intermedia* and *A. scoparia* were significantly different (P<0.05; Fig. S4).

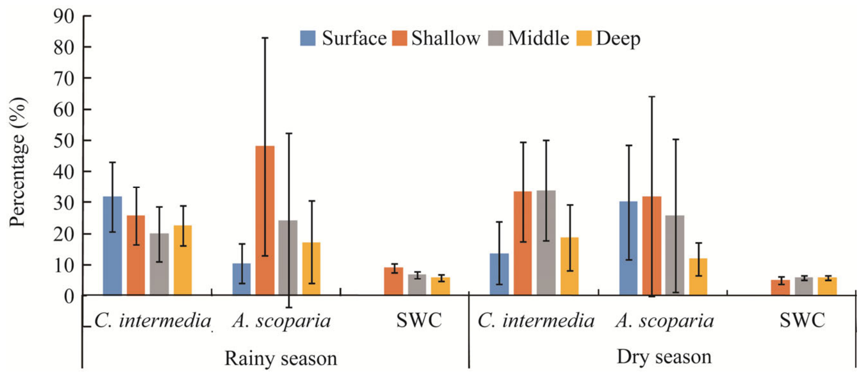

Fig. 4 Water uptake percentage from different potential sources for *Caragana intermedia* and *Artemisia scoparia* in the rainy and dry seasons during 2016–2017. Water sources were defined as BSCs (biological soil crusts) ranging from surface (0–2 cm), shallow (2–30 cm), middle (30–70 cm) to deep (>70 cm). SWC, soil water content. Bars are standard errors.

3.4 Root length distribution of *C. intermedia* in 0–10 cm soil layer

BSCs also affected root distribution of *C. intermedia* (Figs. 5 and S1). More fine roots occurred in 0–5 cm layer in the presence of BSCs than without them (P<0.05), but this difference was not observed in 5–10 cm layer (P>0.05). Overall, more fine roots were found in 0–5 cm layer than in 5–10 cm layer in both plots, but the difference was not significant (P>0.05).

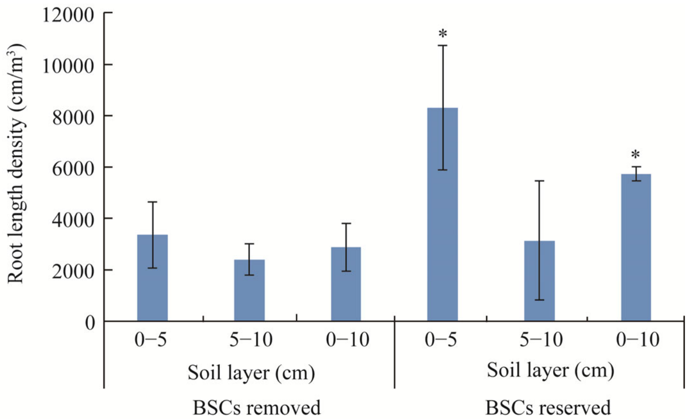

Fig. 5 Fine root length density in 0–10 cm soil layer for *Caragana intermedia* in plots with (BSCs reserved) and without biological soil crusts (BSCs removed). Fine roots were defined as roots with a diameter within 0.5–2.0 mm. *, P<0.05 level. Bars are standard errors.

4 Discussion

4.1 Surface soil water use by *C. intermedia*

Whether *C. intermedia* can use more of the surface soil water when BSCs covered depends on two conditions, one is the availability of water, and another is the fine roots in the surface soil. Firstly, the relative availability of surface soil water was increased when BSCs covered (Fig. 2), as has been similarly observed in desert regions (Li et al., 2010). Secondly, more fine roots of *C. intermedia* were found in 0–5 cm layer in the presence of BSCs (Fig. 5). Although BSCs exacerbated the degree of soil water deficiency in 0–300 cm layer, BSCs also increased the possibility for *C. intermedia* to use more of the surface soil water, just as did *Caragana korshinskii* Kom. in the desert (Zhang et al., 2006) and *C. intermedia* in a loess region (Lu et al., 2017).

The hydrological role of BSCs and their ecological impacts on plant communities in arid and

semi-arid grassland ecosystems are still under debate (Kowaljow and Fernández, 2011; Kidron et al., 2012). The water use pattern of *C. intermedia* induced by BSCs in the desert steppe, just as previous debates, reflects the complexity and particularity of the relationship between soil and vegetation across different regions as BSCs existing. Moss, as the main component of BSCs, are often associated with a high water-holding capacity, which increases the residence time of water in the surface soil, resulting in greater availability for plants with shallow roots (Li et al., 2010). However, *C. intermedia* is a typical shrub with distinct vertical and horizontal roots, which are highly plastic in their response to different soil and water conditions (functionally dimorphic root system, Grossiord et al., 2017). Many shrub species develop horizontal roots in drier soil habitats (Zhang et al., 2010; Zhu et al., 2010) so as to utilize shallower soil water (Jia et al., 2012; Liu et al., 2012). As has been previously reported (Zhou et al., 2013; Lu et al., 2017), water used by both shrubs and grass may be obtained from different soil layers according to changes in water availability during different seasons. In our study, the distribution of fine roots in 0–5 cm soil layer indicates that *C. intermedia* also has the ability to use the surface soil water.

However, due to limitations in observational techniques, we do not have direct evidence of the existence of *C. intermedia* fine roots in BSCs themselves. It is also possible that the dense structure of moss does not allow the roots of *C. intermedia* to enter (Galun et al., 1982). In fact, the isotope ^{18}O signal between BSCs (0–2 cm) and the surface soil layer (0–5 cm) may be indistinguishable, due to the close physical and hydrological connection between them (Chamizo et al., 2012). Therefore, the water source indicated by the isotope analysis may reflect the utilization of water in the surface soil layer (possibly including BSCs) by *C. intermedia*, which is more consistent with the distribution of water and roots.

4.2 Seasonal water use patterns of coexisting plants

In arid regions, most plants preferentially use shallow soil water, and too deep soil water might be only used as a supplementary source (Eggemeyer et al., 2009; Liu et al., 2014), depending on the relationship between supply (distribution of soil water) and demand (distribution of root system). At the same time, the extensive distribution of roots in the surface layer can compensate for the relative deficiency of soil water and minimize energy expenditure (Ogle and Reynolds, 2004; Schenk, 2008). That is, spatial overlap of water source for most species in arid regions generally cannot be avoided (Ehleringer et al., 1991). In our study, water in the 0–30 cm soil layers is the main source for both *C. intermedia* and *A. scoparia*, accounting for close to 60% of total usage. This indicates spatial overlap in the shallow soil layer and therefore water competition between the shrub and grass are not avoided.

However, there are obvious differences in water sources between dry season and rainy season both for *C. intermedia* and *A. scoparia*. For *C. intermedia*, 13.7% of water was obtained from BSCs and 33.5% was drawn from the shallow soil layer during dry season; the same values are 30.2% and 31.9% for *A. scoparia*. Meanwhile, in the rainy season, these values are 31.8% and 25.7% for *C. intermedia*, and 10.5% and 48.1% for *A. scoparia*. The competitive relationship between species for water resources is related to the soil hydrological environment and seasonal changes in precipitation in arid areas, as well as to life history characteristics of various species (Asbjornsen et al., 2007). In the dry season, *C. intermedia* sprouts earlier than *A. scoparia* (Liang et al., 2008), and has chances to use the deeper soil water coming from the storage of precipitation in the late autumn (Niu et al., 2003; Lu et al., 2017). However, the early growth of *A. scoparia* mainly occurs in the roots as an annual plant (Chen et al., 2019), and its soil water use gradually increases in layer. Therefore, there may not be many opportunities for the fine roots of the two plants to directly interact in the early dry season. Other studies have shown that under drought conditions, herbs generally adopt physiological adaptation to reduce water consumption, while shrubs would search more of water sources so as to more actively respond to drought (Angert et al., 2009; Chen et al., 2017; Lu et al., 2017). Therefore, in cases of water source overlap in space, *C. intermedia* and *A. scoparia* may still coexist through various means such as seasonal water division and life history differences.

At the same time, the existences of BSCs significantly affected the hydrological characteristics and water environment of the surface soil, which made it possible to further divide the shared soil water resource for *C. intermedia* and *A. scoparia*. In the study area, the biological activity and hydrological characteristics of BSCs were significantly different between the arid and rainy seasons. In general, the water-holding capacity of BSCs is greater in the dry season; contrastingly, the water-infiltrating capacity of BSCs is greater in the rainy season (Zhang et al., 2014; Yang et al., 2018). More precipitation may be contained in the surface soil in the dry season, and therefore *A. scoparia* has a chance to use the water, rather than *C. intermedia* in the dry season. However, for both *C. intermedia* and *A. scoparia,* more fine roots are invested in the surface soil layer during the rainy season to intercept water filtering through the BSCs, with the improvement of surface soil moisture conditions.

Here, different with the classic shrub-grass coexistence mechanism of "upper and lower layers" (it means that shrub use the water in lower soil layers, and grass use that in the upper soil layers), the division of water resources between the shrub and grass still can be realized based on the differences of their life history when BSCs are present, even if the main sources of water for shrubs and grasses are highly concentrated in the shallow soil layers.

5 Conclusions

When the surface soil was covered by BSCs, it exacerbated the average degree of soil drought in 0–300 cm layer as a whole, but the relative availability of water in the surface soil layer (0–5 cm) also increased, since more water was contained in the layer. The surface soil, including BSCs where possible, might be a key water source used by *C. intermedia.* In cases where the main sources of water for *C. intermedia* and *A. scoparia* were both concentrated in the shallow soil layer (0–30 cm), division of water resources also can be achieved for *C. intermedia* and *A. scoparia* based on the differences of life history. The coexistence for *C. intermedia* and *A. scoparia* around the competition of shallow soil water with the covering of BSCs, breaks through the "up and down" mode of shrub-grass coexistence in arid areas. Different with the result from BSCs in desert areas, the natural withdrawal of artificial *C. intermedia* from desert steppe will be a long-term process, and the highly competitive relationship between shrubs and grasses also determines that its habitat will be maintained in serious drought state for a long time.

Acknowledgements

This research was funded by the National Natural Science Foundation of China (32060313, 31760707). We sincerely appreciate Mr. GU Junlong, Mr. YANG Dongdong, and Mrs. MIAO Fan, whose significant contributions to field investigations made the manuscript possible.

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Appendix

Table S1 Shrub morphological characters and biodiversity in S-CK and S-BSC

Plot	Shrub morphological characters				Biodiversity index			
	CA (m^2)	SH (m)	BD (cm)	CD (%)	*R*	*H*	*D*	*E*
S-CK	2.87±0.30	1.25±0.43	1.79±0.63	23.5±4.08	2.33±0.12	3.38±0.36	0.23±0.17	1.25±0.12
S-BSC	2.51±0.45	0.99±0.28	1.47±0.42	21.8±5.22	1.55±0.06	2.43±0.40	0.40±0.09	0.98±0.15

Note: CA, canopy area; SH, shrub height; BD, base diameter of branch; CD, covering degree; *R*, richness index; *H*, Shannon-Wiener index; *D*, dominance index; *E*, evenness index; S-CK, shrubland without BSCs (biological soil crusts) cover; S-BSC, shrubland with BSCs cover. Mean±SD.

Table S2 Information of surface soil (0–20 cm) in S-CK and S-BSC

Plot	Silt and clay (%)	SOC (g/kg)	TN (g/kg)	TP (g/kg)
S-CK	11.08±5.08[a]	3.94±0.35[a]	0.29±0.07[a]	0.29±0.06[a]
S-BSC	15.44±7.04[a]	4.04±0.27[a]	0.23±0.06[a]	0.33±0.02[a]

Note: Different lowercase letters within the column represent significant differences between S-CK and S-BSC at $P<0.05$ level. S-CK, shrubland without BSCs (biological soil crusts) cover; S-BSC, shrubland with BSCs cover. Mean±SD.

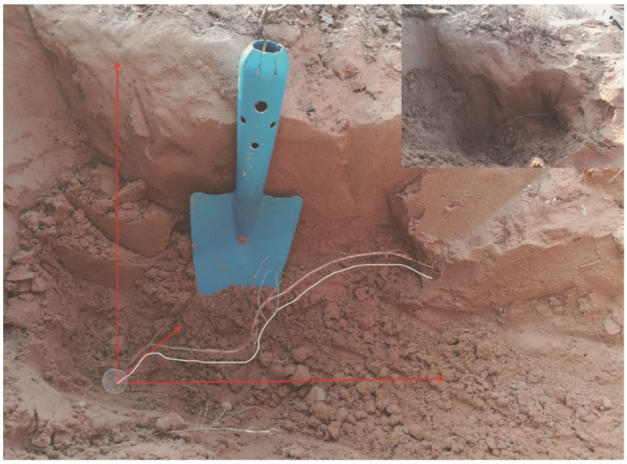

Fig. S1 Upper-direct growth of roots in 0–20 cm soil layer for *C. intermedia* in the rainy season in 2018

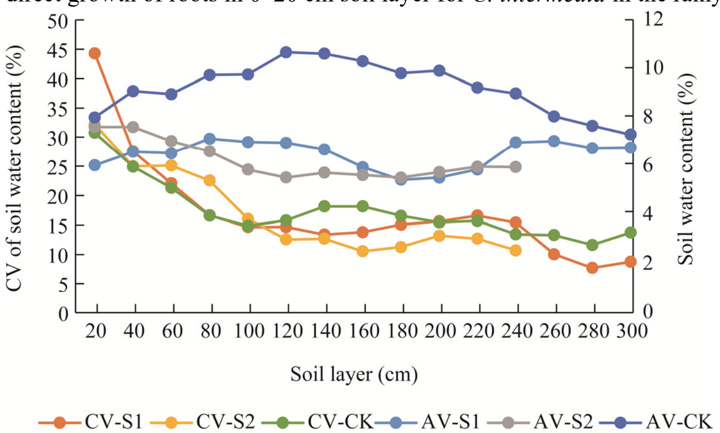

Fig. S2 Soil water content and its CV (coefficient of variation) values in different soil layers during 2012–2017. CV-S1, CV values of soil water contents during 2012–2017 in S-CK plot; CV-S2, CV values of soil water contents during 2012–2017 in S-BSC plot; CV-CK, CV values of soil water contents during 2012–2017 in CK plot; AV-S1, average values of soil water contents during 2012–2017 in S-CK plot (shrubland without BSCs cover); AV-S2, average values of soil water contents during 2012–2017 in S-BSC plot (shrubland with BSCs cover); AV-CK, average values of soil water contents during 2012–2017 in CK plot (grassland without shrub).

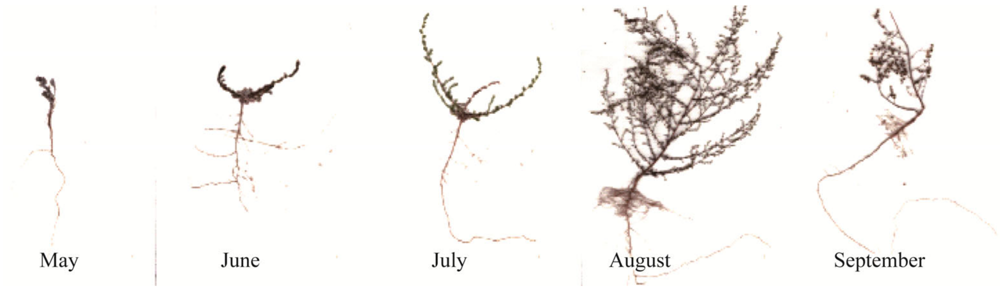

Fig. S3 Root growth of *A. scoparia* from May to September

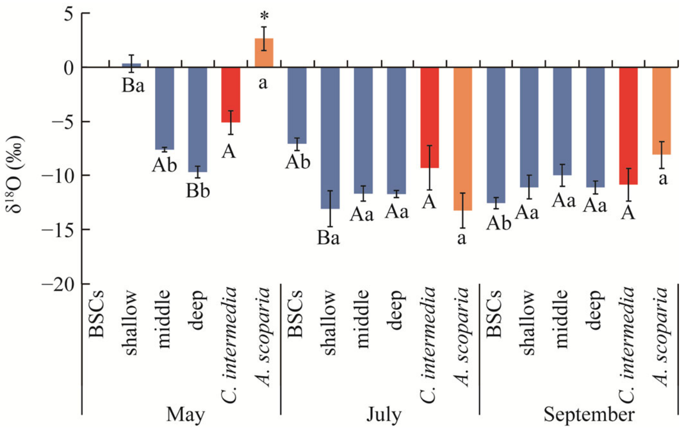

Fig. S4 Percentage of water uptake from four potential soil water sources for *Caragana intermedia* and *Artemisia scoparia* in the rainy and dry seasons during 2016–2017. Water sources were defined as BSCs (biological soil crusts) ranging from surface (0–2 cm), shallow (2–30 cm), middle (30–70 cm) to deep (>70 cm). Different uppercase letters indicate significant differences between *C. intermedia* and different water sources at $P<0.05$ level. Different lowercase letters indicate significant differences between *A. scoparia* and different water sources at $P<0.05$ level. * indicates significant differences between *C. intermedia* and *A. scoparia* at $P<0.05$ level. Bars are standard errors.